ARE THE EXTRINSIC MUSCLES OF THE AIR-BLADDER IN SOME SILUROIDÆ AND THE "ELASTIC SPRING" APPARATUS OF OTHERS SUBORDINATE TO THE VOLUNTARY PRODUCTION OF SOUNDS? WHAT IS, ACCORDING TO OUR PRESENT KNOWLEDGE, THE FUNCTION OF THE WEBERIAN OSSICLES? A CONTRIBUTION TO THE BIOLOGY OF FISHES.

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Τῶν πόνων πωλοῦσιν ἡμῖν πάντα τ'αγάθ οἱ θεοί.
(Επίχαρμος.)

HAVING seen from a memoir by Professors Bridge and Haddon, in the *Proceedings of the Royal Society*[1] (Ia1), which was evidently the preliminary of a more extensive work, that these naturalists were engaged in studies of the anatomy of the Siluroidæ, and especially with that of the air-bladder and the modified vertebræ of these fishes, I took the liberty to forward, on February 9, 1891, to each of the said gentlemen a copy of two of my papers. I had treated in the former[2] of these papers the sound-producing organs in fishes; in the latter[3] the morphology of certain parts of the skeleton of fishes. In the former the Siluroidæ had precisely been the fishes from which I started my investigations. In the latter the conditions in the Siluroidæ, as the title of the paper shows, had been the principal object of my studies.

[1] Ia1: Bridge, T. W., and Haddon, A. C., "Contributions to the Anatomy of Fishes. I. The Air-Bladder and Weberian Ossicles in the Siluridæ" (*Proc. Roy. Soc. Lond.*, xlvi., 1890, No. 283, pp. 309–328). Ia2: Bridge, J. W., and Haddon, A. C., "Contributions to the Anatomy of Fishes. II. The Air-Bladder and Weberian Ossicles in the Siluroid Fishes" (*Ibid.*, vol. lii., 1892, pp. 139–157.) The latter of these two papers I have read since the first sheet of this memoir of mine was in print.

[2] IIb: Sörensen, William, *Om Lydorganer hos Fiske: En physiologisk og comparativ-anatomisk Undersögelse.* [On Sound-producing Organs in Fishes: A physiological and comparative anatomical examination.] Kjöbenhavn, 1884.

[3] III: Sörensen, William, *Om Forbeninger i Svömmeblæren, Pleura og Aortas Væg og Sammensmeltning deraf med Hvirvelsöjlen særlig hos Siluroiderne, samt de saakaldte Weberske Knoglers Morphologi.* [On Ossifications of the Air-Bladder, the Pleura, and the Wall of the Aorta, and their Fusion with the Vertebral Column, especially in the Siluroidæ, together with the Morphology of the so-called Weberian Ossicles.] *Avec un résumé en Français.* (*Danske Vidensk. Selsk. Skr.* 6 *R. Nat.-math.* Cl. Bd. vi. 2, Kjöbenhavn, 1890, pp. 67–152.)

Last summer Professors Bridge and Haddon published a voluminous work,[1] containing their anatomical studies of the Siluroidæ, a work which, on account of the evident diligence and ability displayed, as well as from the great number of fishes treated, will be for a long period a most important work in the anatomy of the organs in question.

Dr. Lütken, Professor of Zoology at the University of Copenhagen, has been so kind as to lend me his copy of this work, and I have thus been fortunate to make myself acquainted with its contents a long while before I should otherwise have been able to do so. It has been a great satisfaction to me to see that these two naturalists agree with me as to the morphological interpretation of the skeletal parts, as well in their morphological summary (pp. 224–261), as now and again in the special description of the fishes, and that they share the opinions I have suggested in my last work, of which they have evidently perused the "resumé en français." Nowhere, as far as I can see, have they urged any objections to the views I have set forth. However, I take the liberty to remark that the reports they have made of this paper of mine are not quite reliable,—a circumstance which is evidently due to their difficulty in interpreting the Danish language, nearly related though it be with the English. Thus they relate (p. 260) that I consider the "claustrum" as the neural spine of the first vertebra; the "stapes" (scaphium, Br. and Hadd.) as the neural arch of the first vertebra; the "incus" (intercalarium, Br. and Hadd.) as the neural arch of the second vertebra; the "malleus" (tripus, Br. and Hadd.) as the rib of the third vertebra. But such is not exactly my opinion of these skeletal parts. As to the "claustrum," on the contrary, I have been careful not to call it a neural spine, and I have shown that at the first 3 or 4 vertebræ in the Ostariophyseæ[2] (in other Physostomi only at

[1] *Ib:* Bridge, T. W., and Haddon, A. C., "Contributions to the Anatomy of Fishes. II. The Air-Bladder and Weberian Ossicles in the Siluroid Fishes" (*Phil. Trans. Roy. Soc. Lond.*, vol. clxxxiv., 1893, B., pp. 65–333).

[2] The name given to all families furnished with the Weberian ossicles by Sagemehl (p. 22). [IV: Sagemehl, M., "Beiträge zur vergleichenden Anatomie der Fische. III. Das Cranium der Characiniden nebst allgemeinen Bemerkungen über die mit einem Weberschen Apparat versehenen Physostomen-Familien" (in *Morphol. Jahrbuch.* x., Leipzig, 1885, pp. 1–119). With great force Sagemehl (*ib.*, p. 9) denies the existence of the Weberian ossicles in the Gymnarchidæ, which Bridge and Haddon count among the Ostariophyseæ. I have not examined the *Gymnarchus niloticus.*]

the first vertebra) there exists a separate ossicle, which sometimes forms part, sometimes not, of the spinal canal, and which, as far as I can judge, is homologous with the ossa imparia in the Acipenser.

After having mentioned the Weberian ossicles in each of the families belonging to the Ostariophyseæ, I have, to facilitate the survey, compiled the following table (III. p. 105):—

<table>
<tr><th></th><th>Characini.</th><th>Cyprinoidei.</th><th>Cobitini.</th><th>Gymnotini.</th><th>Siluroidæ.</th></tr>
<tr><td>Claustrum.</td><td colspan="3">The os commissurale of the 1st vertebra.</td><td>Is wanting.</td><td>The os commissurale of the 1st vertebra is often wanting.</td></tr>
<tr><td>Stapes.</td><td colspan="5">The neural arch of the 1st vertebra.</td></tr>
<tr><td>Incus.</td><td colspan="2">The neural arch of the 2nd vertebra + ossified ligament.</td><td colspan="3">Only ossified ligament.</td></tr>
<tr><td>Malleus.</td><td>The rib of the 3rd vertebra + the basal part[1] of the rib + ossified air-bladder + ossified ligament.</td><td colspan="3">The rib of the 3rd vertebra + ossified air-bladder + ossified ligament.</td><td>In Clarias and Plecostomus the rib of the 3rd vertebra + ossified air-bladder + ossified ligament. In the other genera [known to me] the rib of the 3rd vertebra + the basal part[1] of the rib + ossified air-bladder + ossified ligament.</td></tr>
<tr><td>Os suspensorium mihi [sc. vesicæ natatoriæ].</td><td colspan="4">The basal part[1] of the rib of the 4th vertebra + ossified air-bladder.</td><td>Shares this function with other bones.</td></tr>
</table>

To whosoever has read, and were it only this table, it will be quite evident that my views as to the morphology of these

[1] Or the processus transversus.

ossicles are recorded by Professors Bridge and Haddon in a very superficial manner.

In all the (nine) genera of the Siluroidæ which I have examined, the "incus" in full-grown specimens consists of ossified ligament; but Bridge and Haddon have made the very interesting discovery that this ossicle forms a smaller or larger part of the neural canal in some genera (*e.g.*, Macrones, Liocassis, Pseudobagrus, Bagroides—Cryptopterus, Callichrous), in which respect these genera approach to the other families of the Ostariophyseæ.

When, however, Bridge and Haddon say (I*b*, p. 261):—

"A further question arises as to whether, in addition to a modified neural arch, the intercalarium [incus, Web.] did not originally include an element comparable to a transverse process. We are inclined to think that it did, and that the horizontal process of the ossicle, when present, represents the modified transverse process of the second vertebra. In its origin from the neural arch or ascending process, the horizontal process conforms precisely to the contiguous transverse processes of the fourth and fifth vertebræ, which spring in exactly the same way from the neural arches, and not from the centra of their respective vertebræ."

I may answer this question in the negative, because in fact I have already done so—a circumstance which, however, the authors had not observed, as they had not made themselves acquainted with the *Danish* part of my paper in question, in which is set forth the documentation of my morphological views. 1°. In the other families of the Ostariophyseæ, at the 2nd vertebra, there exists, besides the "incus" when present, a real[1] transverse process; nay, in the Gymnotini this process even carries a rib. 2°. A transverse process (or rib) in fishes always springs from the centrum of the vertebra, and never from the neural arch; when it seems to do so, it is only so in appearance. And to abide by the Siluroidæ, one glance at the figure (*Tb.* I. fig. 10) which I have given of this part of the vertebral column in the fœtus of *Galeichthys feliceps* also proves how the transverse processes of the (real) 4th and 5th vertebræ spring from the centra of their respective vertebræ, while the proximal end of the "incus" is fixed in the wall of the neural channel. And, starting from this fœtus, I have proved (III. pp. 101, 102) that

[1] I must add this designation, as on the 1st vertebra in the Cyprinoidei there exists a transverse process, which is false.

when the transverse processes of the normal vertebræ in the Siluroidæ *seem* to spring both from the centrum and the arch of their vertebra, this is due to a later ossification of the ligaments which—as in other fishes—unite the transverse processes (or ribs) with the neural arch. And I may add that when the modified transverse processes of the (real) 4th and 5th vertebræ seem to spring from the neural arches, this is equally due to a secondary transformation during the growth (in the very young animal), as briefly intimated in my paper (pp. 103–105). The "horizontal process" of the "incus" is ossified ligament.

Professors Bridge and Haddon say (*Ib*, p. 249), that in Clarias "the inferior limb" of the "post-temporal" "becomes quite rudimentary, and loses its usual articulation with the basi-occipital." On the contrary, I have declared that this "inferior limb" does not exist at all in this genus. This might seem but a very slight difference. To be sure, the difference of expression is very slight, but the difference as to the interpretation of the fact in question is anything but slight. For, as I have shown,—a fact also mentioned by Bridge and Haddon,—this "inferior limb" is a very essential point of the skeletal structure of the Siluroidæ. But what is this "inferior limb"? In most of the Teleostean Fishes the "pectoral girdle"—as is well-known—consists of three bones, called by Cuvier the "suprascapula," the "scapula," and the "humerus." As is equally well known, the uppermost of these bones is, as a rule, joined with two bones of the skull, viz., with the os squamosum (or temporale), and with the epioticum (or paroccipitale). The bone in the middle, in the Siluroidæ coalesced with the uppermost one to form the "suprascapula" (Cuvier), or the "post-temporal" (Br. and Hadd.), is—a fact[1] less well known—in most Fishes, also in Amia and Polypterus, united, as a rule,

[1] For this reason I have had the ligament drawn in all the figures I have published, where it was possible to do so. The only author who has mentioned it is, as far as I know, Mettenheimer, C., *Disquisitiones Anatomico-comparativæ de membro piscium pectorali*, Berolini, 1847. This ligament is also ossified in Dactylopterus (where it acts the same part as in the Siluroidæ), Aulostoma, and Ostracion (but not in Batrachus tau). This also appears to be the case in Lepidosiren, Protopterus, and Ceratodus. But as I have dissected none of these genera, I dare not state with certitude that the bone ("the first rib," Günther) which unites the first vertebra or the basis-cranii with the "shoulder-girdle" is homologous with the said ligament.

with the occipitale basilare, or uncommonly, as in the Cyprinoidei and the Gadoidæ, with the centrum of the 1st vertebra. But while the junction between the "suprascapula" and the epioticum is brought about by means of a slender process of the suprascapula — *i.e.*, an ossified ligament — in most cases the junction between the lower end of the scapula and the occipitale basilare, or the centrum of the 1st vertebra, is brought about by means of a ligament. For it is but rarely the case that the latter is ossified: in the Cyprinoidei a shorter or longer part of it is ossified; and as the ossification takes its beginning from the proximal end, it has the appearance of being a "transverse process" of the 1st vertebra; but in nearly all the Siluroidæ (viz., with the exception of Clarias) this ligament is a more or less considerable bone, the strength of which, as well as the manner in which it is connected with the occipitale, is in relation to the size of the first ray of the pectoral fin, and whether the "suprascapula" is connected with the transverse process of the (real) 4th vertebra or no. Ten years ago I had already pointed out this fact in my first paper (II*b*, pp. 3 and 21). And in both my papers I have proved that in Clarias there exists no connection whatever between the "suprascapula" and the occipitale basilare, because the said ligament has not been able to form itself, the accessory gill-cavity, in which the air-breathing dendritic organs are inclosed, being placed where the ligament should be, and has therefore, if I may say so, supplanted it. In return, the pectoral girdle has in this genus been strengthened by the helmet (the dermoidal bones) having attained to a size unparalleled in all other Siluroidæ except when the large (2nd) ray of the dorsal fin is a very effective weapon—in Clarias it is no weapon at all, but a mere weak ray, and the preceding "rudimentary" ray is here wanting.

If the authors had known the true nature of this "inferior limb" of the post-temporal, and the importance of the degree of the development of this bone in these animals, they would never have been "tempted to think that the post-temporal plates of Macrones and the allied genera might represent a form of 'elastic spring' mechanism" (p. 245). For, neither from a morphological nor from a physiological point of view, have these two things anything to do with each other. But, as I shall

prove in the following pages, the authors had, in their Memoir in the *Transactions* of the Royal Society, completely overlooked my first paper.

I.

Are the extrinsic muscles of the air-bladder in some Siluroidæ and the "elastic spring" apparatus of others, subordinate to the voluntary production of sounds?

> Πάντα δὲ ταῦτα τὴν δοκοῦσαν φωνὴν ἀφιᾶσι . . . τὰ δὲ τοῖς ἐντὸς τοῖς περὶ τὴν κοιλίαν. Πνεῦμα γὰρ ἔχει τούτων ἕκαστον, ὃ προστρίβοντα καὶ κινοῦντα ποιεῖ τοὺς ψόφους.
>
> —*Aristotle.*

While Professors Bridge and Haddon agree with me in the opinions I have propounded as to the morphology of the skeletal elements treated in my second paper (III.), I cannot, I am sorry to say, pride myself on this concurrence as to the physiology of the air-bladder in the Siluroidæ treated in my first paper (II*b*). In order to show this, I shall take the liberty to quote some remarks by the said authors in their detailed account of the "Physiology of the Air-bladder and Weberian Ossicles in the Siluridæ" (I*b*, pp. 261–303). Page 269:—

"In addition to the various other methods by which voluntary sounds are produced in different fishes, the air-bladder not unfrequently shares in the function of phonation. Such sounds are either produced by the vibration of the internal annular diaphragm (Moreau), or by the vibration of certain extrinsic muscles (Dufossé [1]), the air-bladder in the latter case intensifying the sound produced by acting as a resonator. Dufossé (*loc. cit.*) is also of opinion that some Ostariophyseæ (*e.g.*, some Cyprinidæ and one or two Siluridæ) produce breathing noises ('les bruits de souffle') by the expulsion of gas from the air-bladder through the ductus pneumaticus, and it has been suggested [2] that the grunting sounds emitted by Clarias have

[1] The first paper of this author here referred to. (V*a*: Dufossé, *Recherches sur les bruits et les sons expressifs que font entendre les Poissons d'Europe . . . Annales d. Sci. Nat. 5 Sér.*, T. xix. Paris, 1874. Art. No. 5.)

[2] By whom?—Day, to whom Bridge and Haddon refer in a paper entitled "Instincts and Emotions in Fishes" (*Jour. Linn. Soc.*, xv., 1881, pp. 31–58) only says as follows:—"Sir Emerson Tennent observed that a Siluroid fish (Clarias) found in the lake at Colombo is said by the fishermen to make a grunt

a similar origin. *The possibility that the Weberian ossicles have any thing whatever to do with phonation, either in the Siluridæ or in other Ostariophyseæ, is very remote,*[1] and need be but briefly considered."

Page 270: "We are strongly inclined to the opinion that although sounds may indirectly have their origin in the air-bladder, *they have no relation to it other than as accidental accompaniments in the exercise of its normal hydrostatic function,*"—with the following footnote: "For these reasons, and *in the absence of definite experimental evidence*, we cannot at present accept Sörensen's *ingenious theory* that the extrinsic muscles of the air-bladder in the Pimelodinæ, and the 'elastic-spring' apparatus of other Siluridæ, are solely subordinate to the voluntary production of sounds." "In one example cited above (Clarias) it is almost certain that the grunting sound which the fish is said to make could not be caused *by the voluntary expulsion of gas from the air-bladder*, inasmuch as this organ is not only rudimentary, but almost completely encapsuled by bone. Eliminating such doubtful examples of the association of the air-bladder with phonation in a few Siluridæ and Cyprinidæ, it may be urged with regard to the rest that the comparative[2] rarity of *well authenticated instances of the production of voluntary sounds*, the absence of extrinsic muscles in all but a few genera (Pimelodinæ), and *the want of internal vibratory diaphragms, or other obviously vocal structures, are quite sufficient to prove that the air-bladder takes little or no part in this function, at all events, by any of the ordinary methods known in other Fishes.*"

P. 296: "In the great majority of the Ostariophyseæ the escape of air from the air-bladder through the ductus pneumaticus apparently takes place only as the result of the expansion of the contained gases under the influence of diminished hydrostatic pressure, although it is possible that the rate of overflow may in some way be regulated. In some few Siluridæ, however, there does seem to exist a special

under water when disturbed." And in saying so he is almost literally quoting Sir Emerson Tennent, whose words run as follows (*Ceylon.* Fifth edition, vol. ii., Lond. 1860, p. 470):—"The fishermen assert that a fish, about five inches in length, found in the lake at Colombo, and called by them 'Magoora,' makes a grunt when disturbed under water." Bridge and Haddon, indeed, quote a paper by Day bearing the very same title, and to be found in the *Transactions of the Zool. Soc.*, vol. xv., 1880; but nowhere in the *Transactions* of this Society, neither in vol. xv. nor in the volume published in 1880, there exists such a paper. I therefore presume that they refer to the paper which I have mentioned, the more so as *the references in the physiological division of their work*, with the exception of the references to their own papers, to those of Ramsay Wright, and to Günther's "Introduction," are wanting in precision.

[1] The italics in this and the following quotations are mine.

[2] The Siluroidæ are, among all families of Fishes, the one which, before the time of Dufossé, counted the greatest number of species known as sound-producing—both Platystoma Orbignyanum, Pseudaroides clarias, and 2-3 species of the genus Doras, for instance, were known as such by Cuvier and Valenciennes. The statements of naturalists as d'Orbigny and Charles Darwin, Professors Bridge and Haddon, will not, I suppose, design as being not "well authenticated."

mechanism *by which, under certain conditions, the air-bladder may be subjected to considerable compression, and the air which it contains either forcibly expelled, or greatly reduced in volume by condensation* [Moreau!].[1] This mechanism presents two important modifications, viz., the "elastic spring apparatus" and the powerful extrinsic muscles of the Pimelodinæ."

Pp. 297–298:—"The mobility and elasticity of the transverse process which forms each spring will certainly give to the lateral portions of the anterior wall that capacity for sharing in the distension of the anterior chamber which is prevented in all other Siluridæ by the absolute rigidity of the processes in question, but it is at the same time, equally clear that the 'elastic spring' apparatus cannot possibly give the fish any power of directly compressing the air-bladder, except under certain conditions, viz., when the anterior chamber becomes distended through the diminution of pressure which occurs in movements of ascent, coincidently with the forward movement of the two springs as the result of the voluntary or reflex contraction of their protractor muscles. Under such circumstances the [elastic spring,] mechanism potentially acquires the power to modify the capacity of the air-bladder, for the subsequent relaxation of the muscles will at once enable the springs, through the force of their own recoil, to exert their full strength in compressing both the air-bladder and its gaseous contents." And to the words "gaseous contents" is added in the form of a footnote:—"Should this view of the mode of action of the 'elastic spring' apparatus prove correct, *it will be difficult to see how the mechanism can have anything to do with the production of voluntary sounds*, as suggested by Sörensen, *inasmuch as the Fish would only be able to exercise its vocal powers under conditions involving pressure reduction during ascent from a deeper to a more superficial level. Under such conditions only does it seem likely that the contained gases would be expelled with sufficient force to produce any definite or characteristic sounds.*"

P. 300:—"The Extrinsic Muscles of the Air-bladder in the Pimelodinæ.—A function substantially similar to that of the 'elastic spring' apparatus may, in all probability, be assigned to the powerful

[1] The authors have perused Moreau's paper (VI. Moreau, A.: "Recherches expérimentales sur les fonctions de la vessie natatoire": *Annales d. Sci. Nat.*, *6 Sér.*, T. iv. Paris, 1876. Art. No. 8), but they have not *studied* this most excellent memoir. Otherwise, they would have noticed his remarks (p. 52) which may regard also the theory of Joh. Müller about the function of the "elastic spring" apparatus in some Siluroidæ: "L'attention des savants n'avait pas été encore fortement appelée sur les phénomènes de la contraction musculaire sur la fatigue que le travail musculaire engendre et par conséquent sur l'invraisemblance d'efforts aussi prolongés et aussi énergiques que ceux que suppose la théorie traditionelle." For the very same objection may be urged against the above-cited opinion, nay, against all suggested by Bridge and Haddon on the function of the "compressor" muscles and the "elastic spring" mechanism. In the passages of these authors which I am going to quote on the following pages, I take the liberty to add the word ["Moreau!"] to similar remarks.

compressor muscles of the Pimelodinæ.[1] *These muscles cannot possibly have any share in dilating the air-bladder* and rarefying the contained gases in order to facilitate ascent, but it would certainly seem that they enable these particular Siluridæ to exercise a still more effective control over its distension, *inasmuch as the muscles are apparently able to compress the air-bladder at all times*, although more effectively, no doubt, when the latter is more or less distended [Moreau !]. By the contraction of these muscles during rapid movements of ascent the tendency to over-distension on the part of the air-bladder will be promptly counteracted, while a forcible expulsion of gas through the pneumatic duct would enable the Fish to speedily adjust its volume and specific gravity to a new plane of least effort at the more superficial level. . . . . In both series of Fishes it is extremely interesting to recall the existence of a special arrangement by means of which the compression of the air-bladder, either by the action of the 'elastic springs' or by the contraction of special *compressor* muscles, is prevented from imparting a too violent shock to the Weberian mechanism, and more especially to the fluids and sensory epithelia of the internal ear. . . . . *The extreme difficulty of attempting to arrive at a satisfactory solution of* the various problems arising out of the physiology of the air-bladder, *through anatomical data alone*, is again forcibly illustrated, for *it is impossible entirely to exclude the possible relation of the extrinsic muscles of the Pimelodinæ to the function of sound production, and it may also be the case, although perhaps less likely, that the same reservation will also apply to the 'elastic spring' mechanism. That a violent expulsion of air from the air-bladder should produce definite sounds is extremely probable*, but how far such sounds can be considered as related to the primary function of these muscles, or as merely accidental concomitants to it, must for the present remain an open question. Sörensen has adopted the former suggestion, and regards both the *compressor* muscles and the 'elastic spring' mechanism as being subordinate to sound production. Nevertheless, *in the absence of confirmatory experimental evidence*, we still think it worth while to direct attention to an alternative interpretation of the function of these structures, which is at least as consistent with their morphology as any other view at present suggested. We have elsewhere (p. 270 and p. 298) suggested certain difficulties, which, in our opinion, are *serious* objections to Sörensen's views on this point."

To everybody who has perused these quotations from the work of Professors Bridge and Haddon, it will now be evident that these authors have set forth the following suggestions:—

1. *That the function of the "protractor" muscles of the "elastic spring" mechanism in some Siluroidæ consists in pulling forward*

[1] I beg to direct the attention of the reader to the fact, that, as will appear from the above quotation, the authors are of opinion that the effect produced by the protractor muscles of the "elastic spring" apparatus is nearly quite the reverse of the effect produced by the extrinsic muscles of the Pimelodina.

the springs, in order to enable the air-bladder to distend itself in front, and that the effect which they produce is therefore nearly quite the reverse of the effect produced by the extrinsic muscles, the so-called "compressor" muscles, of some other Siluroidæ.

2. *That all "internal vibratory diaphragms or other obviously vocal structures" are completely wanting* in the air-bladder of these fishes.

3. *That without confirmatory experimental evidence I have propounded a "theory," nay, an "ingenious" one, of the "elastic spring" mechanism and the extrinsic muscles being subordinate to the production of sounds.*

4. *That these sounds are produced by "a violent expulsion of air from the air-bladder."*

5. *That the authors have entirely crushed this theory.*

I am quite willing to acknowledge that they have completely succeeded in doing so. This victory has but one deficiency: that what they have succeeded in conquering, are—the windmills of Montiel! For the opinion which they impute to me, I never had nor suggested.

But why, then, do they impute this theory to me? Firstly, because they had entirely overlooked my book, *Om Lydorganer hos Fiske*, and had not formed an idea as to the contents of this work by perusing its "explicatio figurarum"[1]; and secondly, because, even if they themselves had not been fully aware of the fact, they were under the influence of the first paper, written in modern times, "On the Origin of Sounds produced by Fishes"[2]—a paper by no means worthy of the eminent genius of its author.

In this paper Joh. Müller says:—

"Im Munde jedes Fisches können, wenn er sich in der Luft befindet, Lufttöne entstehen, gleichviel ob er eine Schwimmblase besitzt oder nicht, ob die Schwimmblase geschlossen ist oder einen Luftgang in den Mund besitzt. Dagegen kann bei einem Fische, der unter Wasser tönt, an Lufttöne nur dann gedacht werden, wenn er einen Luftgang der Schwimmblase besitzt und wenn dieser hinreichend weit ist, *um Luft plötzlich auszutreiben.*"

[1] The names of the Siluroidæ, the air-bladders of which are represented among the figures, are, however, recited in their memoir.

[2] VII. Müller, Joh.: Ueber die Fische, welche Töne von sich geben, und die Entstehung dieser Töne (*Archiv f. Anat. u. Physiol.* Berlin, 1857, pp. 249–279).

For as Horace says :—

> Quo semel est imbuta recens, servabit odorem
> Testa diu.

If the authors had perused the Latin "explicatio figurarum" in my paper, they would have observed that wherever I have represented muscles, which make the air-bladder act as a sound-producing organ (if only one pair of such muscles do exist), I have designated each of these muscles as "musculus, cujus contractione *sonat* vesica natatoria," whether the fishes mentioned be furnished[1] with a ductus pneumaticus or no.[2] But how could it have been possible to suggest it as my opinion that (extrinsic or intrinsic) muscles of an air-bladder, *without* a pneumatic duct, might ever be able to produce sounds by "a violent expulsion of the air from the air-bladder"? Or, how could I ever—if I had but the slightest notion of the meaning of the Latin words—say, "*sonat* vesica natatoria," if the contraction of the muscles were to effectuate the expulsion of air from the air-bladder?

But if the authors had only read a short remark of mine in "les Comptes rendus,"[3] or in the "Annals,"[4] where it had been translated from "les Comptes rendus," they would have seen that what I have suggested on the production of sounds by means of the air-bladder in the Siluroidæ[5] in question, is quite different from what they impute to me; for in the passage quoted from the "Annals," my words have been thus translated :[6]—"In the Siluroidæ[5] the anterior portion of the swimming-bladder is drawn alternatively forward and backward by the contraction and relaxation[7] of the muscles. During these movements the air, in passing across the incomplete transverse septa, sets the

[1] Pseudaroides clarias (fig. 45); Synodontis schal (fig. 48).

[2] Diodon hystrix (fig. 49); Batrachus tau (fig. 60); Micropogon undulatus (fig. 61).

[3] II*a*: Sörensen, William, "Sur l'appareil du son chez divers Poissons de l'Amérique du Sud" (*Compt. rend. de l'Acad. d. Sci.*, T. lxxxviii. Paris, 1879, pp. 1042–43).

[4] *Annals a. Mag. of nat. hist.* 5 Ser., vol. iv. London, 1879, pp. 99–100.

[5] Doras maculatus, Platystoma Orbignyanum?, Pseudaroides clarias.—The remark also refers to some genera of the Characini.

[6] I readily agree that, on account of its brevity, this summary is not quite clear. As to the manner in which the production of sounds itself is operated, I do not think, however, that it can easily be misunderstood.

[7] I have not succeeded in finding the correct words to express my idea, as may be seen later on from the quotation of my book.

latter in vibration, and the sound is produced. The height, or rather the depth, is in direct proportion to the rapidity of the vibration of the springs."

And if the authors had known a most valuable paper by the late M. Dufossé[1] on the air-bladder as a sound-producing organ, in a fairly considerable number of Fishes (16 species, 7 genera), all without a pneumatic duct, they would have seen that my "theory" was quite in accordance with the result at which this skilful French author had arrived through his examinations—not in his study, but—of living animals. Then, certainly, the authors would not have said that the production of sound, according to my "theory," was not effectuated "at all events by any of the ordinary methods known in other Fishes." And then they would not have spoken about "the want of internal vibratory diaphragms . . . . . " *inasmuch as they themselves have described and represented such diaphragms* (*the "transverse septa"*) *in a considerable number of Siluroidæ—even to the number of six pairs!*

However, even if the opinion which I had suggested was in accordance with the result obtained by Dufossé in his examinations of living fishes, Professors Bridge and Haddon might be entitled to call my opinion a "theory" if, what they evidently supposed me to have done, I had stayed in Copenhagen and "construirt" my "theory" "aus dem Inneren meines Bewusstseins." For that is exactly the way by which they have arrived at the opinions which they have suggested on the function of the air-bladder and the Weberian ossicles in the Siluroidæ.

So I must ask the reader to observe the full title of my book, *On Sound-Producing Organs in Fishes, a Physiological and Comparative Anatomical Research*, my intention being to intimate, in as few words as possible, that my results had been obtained in both ways—vivisection with regard to some forms, and examination of dead animals with regard to others.

Now, my examinations of Siluroidæ and Characini happen to be the basis of my paper, as I *commenced* these studies at the confluence of the Riacho del Oro with the Rio Paraguay.

[1] *Vb*: Dufossé, "Recherches sur les bruits et les sons expressifs que font entendre les Poissons d'Europe . . . " (*Annales d. Sci. Nat.* 5 Sér., T. xx. Paris, 1874. Art. No. 3).

It must now be investigated whether my opinion about the function of the air-bladder and the extrinsic muscles or the "elastic spring" mechanism be a "theory" or no.

About *Doras maculatus* (Cuv. et Val.), I say in my paper, after having described (pp. 85–87) the structure of the air-bladder (*vide* figs. 1 and 2), as well as the "elastic spring" mechanism and its muscles, and after having pointed out the fact that the "malleus" (in this genus) is also a spring, p. 88, as follows :—

"*Observations on the Production of Sounds.*—When the belly of the recently caught fish is opened, and the intestines with their append-

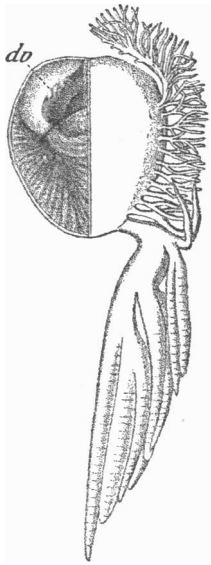

FIG. 1.—*Doras maculatus*, Cuv. et Val. The air-bladder of a specimen, measuring 50 cm. of length, seen from below. Diminished thrice. To the right the ventral wall of the air-bladder has been removed. The cæcal diverticula are not represented on this side. *dv*, one of the circular bony plates (fused with the hinder part of the muscular spring, the transverse process of the (real) 4th vertebra) in the fore end of the wall of the air-bladder. In a living specimen it is not so prominent in proportion to the remaining part of the air-bladder.

ages are taken out quickly, so that the air-bladder is laid open, it may be very easily observed that the air-bladder is in a state of convulsive vibration, at the same time as sounds are produced.[1] This sound

[1] A part from the sounds produced by the movements of the fins.

is a very deep, growling tone, which is so intense that *it is still to be heard very distinctly at a distance of* 100 *feet* [1] when the fish is *out of the water*. In contradistinction from the sound produced by the movements of the pectoral fins, the sound produced by the air-bladder is not discordant, and therefore it is not disagreeable to the ear. As far as I have been able to catch—I am sharp of hearing, but I have some difficulty in distinguishing notes—the air-bladder only commands one tone, but this tone may be more or less strong as it pleases the fish. If you move your fingers backwards and forwards on the air-bladder, you will soon perceive that the vibrating movement, arising at the same time as the sound, is strongest in front, especially near the muscular springs, and likewise that the muscles inserted upon the similar plates of these springs are contracted at the same time as the sound arises. If the muscles are cut asunder, the sound [2] is no more produced. If a small hole is made in the air-bladder (when the muscles are uninjured) the sound does not grow much fainter, but if the hole is enlarged the sound loses considerably in strength. If the

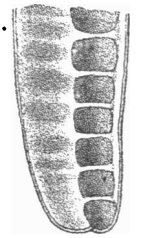

FIG. 2.—*Doras maculatus*, Cuv. et Val. The same specimen. The end of one of the large (posterior) cæcal diverticula of the air-bladder. It is opened, so as to permit a survey of its cellular structure. Natural size.

air-bladder is removed, the sound grows much fainter, but is still audible; then it is exclusively produced by the vibration of the springs. By direct observation I have not been able to prove that the beams of the principal chamber of the air-bladder, or the incomplete transverse septa of its cæcal diverticula, contribute to the production of the sound; but if the reader will compare this with what I am going to communicate in the following pages by *Pseudaroides*, I am of opinion that it will prove *without doubt* that the cæcal diverticula of the air-bladder, on account of the incomplete internal transverse septa (fig. 2), are most intimately concerned in the function of intensifying the sound by means of the air passing forwards and backwards above the septa. By a minute examination it may be observed that the foremost of the bony scutes on the side of the body shares in the vibration when the sound is produced. I presume that the

[1] A Danish foot is a little longer than an English.

[2] Apart from the sounds produced by the movements of the fins.

function of the ligament [1] serving to connect this plate with the circular plate of the muscular spring, does not only consist in transmitting the sounding vibrations of the air-bladder to the water, but also in preventing a too violent reaction of the spring when the muscle is relaxed."

After having described the air-bladder and its extrinsic muscles (p. 92) in *Platystoma Orbignyanum*? Val.[2] and *Pseudaroides clarias*, Bl., and having proved the "malleus" (the "tripus," Br. and Hadd.) to be a spring, I continue (p. 93) as follows :—

"*Observations on the Production of Sounds.*—When the air-bladder of the living animal is laid open, it is very easy to perceive that the muscles in question are contracted at the same time as a strong, deep, growling sound is produced, while the wall of the air-bladder is set into a strong, vibrating motion. The majority of the specimens I have examined of Pseudaroides were not above a total length of 25 to 35 cm. Hence the walls of the air-bladder were not so thick as to prevent me from distinguishing, without opening the air-bladder, the internal transverse septa in the shape of darker transverse stripes; therefore, I was able to observe very distinctly that, during the emission of the sound, they were swinging (or being moved) very quickly to and fro (fig. 3).

This fact is sufficient to prove that they play a very important part in serving to intensify the sound, by means of the air vibrating above their edges from one chamber to another. If a small hole is made in the air-bladder of a Platystoma, the intensity of the sound is not diminished in any remarkable degree. But if a fissure, however small, is made in the air-bladder, the sound grows distinctly fainter, and at last quite ceases, even if the muscles are still in action.

As far as I have been able to observe, as is the case in Doras, only one contraction of the muscles takes place every time a sound is produced. This sound always lasts for a certain time, grows fainter toward the end, but suddenly ceases. On the nature of the sound the same may be said as I have stated about Doras. The sound produced by a Platystoma [3] is audible at a distance of more than 20 feet if the animal is on shore."

[1] This ligament connects the distal circular plate of the "elastic spring" with the foremost, hardly visible, of the thorny dermoidal plates, which in this genus are placed on the side of the body. A corresponding ligament I have not found in any other genus of the Siluroidæ furnished with the "elastic spring" mechanism.

[2] Professor Lütken, who was then so kind as to determine the Siluroidæ which had been the object of my examinations, was not able to determine with exactitude this species, as I had not brought home any uninjured specimens. But at any rate it is *not* Pl. fasciatum, as related by Bridge and Haddon (*Ib*, p. 118). For, according to Joh. Müller, it is easy to distinguish the air-bladder in this species from that which I have examined.

[3] The specimens examined generally had a length of 1 metre, or somewhat less.

I ought to have added that the sound is no more produced when the muscles are cut. Whether, by this operation, I have cut the pair of small muscles (M. "tensores tripodium," Br. and Hadd.) which Bridge and Haddon have always found along with the large extrinsic muscles I do not know, as I have not seen these muscles; I suppose it to be so.

As it was of some importance in connection with the subsequent comparative-anatomical part of my book, I added:—"From the description of the air-bladder of these three genera it is evident that, particularly in Platystoma and Doras, it is so 'cellular' as is but rarely found in fishes; nay, *Doras maculatus*

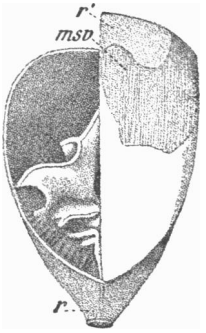

FIG. 3.—*Pseudaroides clarias*, Bl. The air-bladder of a specimen measuring 39 cm. of length, seen from below. To the right the ventral wall of the air-bladder has been removed, so as to permit the survey of the internal transverse septa, which divide its lateral halves into compartments. (By this operation a small part of the septa has been removed.) Diminished twice. *msv*, one of the muscles, which make the air-bladder act as a sound-producing organ; *r*, the kidneys behind the air-bladder, cut off from behind; *r'*, the pronephros.

seems to be of all fishes (perhaps with the exception of Gymnarchus) the one whose air-bladder contains the greatest number of 'cells.'"

As may be observed, this is in perfect accordance with the words of Bridge and Haddon (*Ib*, p. 236):—

"It may be remarked that cæcal appendages are very characteristic of those Siluroids in which an elastic spring 'apparatus' is present."[1] And in this connection it is well worth noticing what the authors add:—"A branching condition of the air-bladder, with the branches

[1] Not, however, in Synodontis, Malapterurus, and Euanemus.

ending in cæcal extremities, is very common in certain Physoclist genera. . . ."—See Günther,[1] p. 144–145.

For the genera mentioned in this place by Dr. Günther belong, with the exception of Polynemus, to the Sciænoidei, which are known to produce sounds by means of the air-bladder.

I myself was also struck with a similar very obvious idea, as may be seen from the following lines, a repetition in nearly the same words of what I wrote ten years ago (II*b*, pp. 107–109): —" Being engaged in the above-mentioned investigations at the mouth of the Riacho del Oro, where it enters Rio Paraguay, I was quite unacquainted with what had been published on this subject. I only knew that *Cottus scorpius*,[2] *Trigla* (*gurnardus*), and *Dactylopterus volitans* are sound-producing. But having arrived at the result that the muscles of the air-bladders, which I had examined, serve to throw the air-bladder into sound-producing vibrations, and that a divided[3] air-bladder offered an improved organ for the production of sounds, I consulted V. Carus (and Gerstaecker's) *Handbuch der Zoologie*, which book was my only literary resource in South America, to see if any sound-producing fishes were mentioned there. This, it is true, was not the case; but as to Dactylopterus, the author

[1] XIII. Günther, A. C. L. G., " Introduction to the Study of Fishes," Edinburgh, 1880. The authors here also refer to Günther's *Catalogue of Fishes in the British Museum*, vol. v. But as this volume only contains Physostome fishes, I do not understand this reference.

[2] I have shown (II*b*, p. 78) that this fish produces sounds by stridulating between the præoperculare and the hyomandibulare. Dufossé (V*b*, pp. 91–103) and Professor L. Landois (in a book, *Thierstimmen*, Freiburg in Breisgau, 1874, published by his brother, Dr. H. Landois) judge the sound emitted by this fish to be due to the vibration of certain muscles. But while Dufossé designs these muscles as ". . . des muscles qui . . . font partie des régions inférieures des appareibs : hyoïdien, branchial et pharyngidien," Landois is of opinion that these muscles are the muscles of the shoulder-girdle. I have had no opportunity to resume this investigation after the perusal of the book of Landois.

[3] In the air-bladder of the Characini, examined by me, there is no further division but the well known one into an anterior and a posterior chamber; in *Platystoma orbignyanum* (?) and *Pseudaroides clarias* (see fig. 3 above) the air-bladder is divided into one large anterior chamber and five to six pair of chambers, growing gradually smaller behind and communicating with each other and with the first chamber by means of, comparatively speaking, large apertures along the lateral wall of the air-bladder; in *Doras maculatus* (see figs. 1 and 2 above) it is but partially divided by a longitudinal incomplete septum, and provided with numerous finger-like cæcal diverticula, among which the largest are incompletely divided in cells.

says (p. 539), "Schwimmblase getheilt, mit Muskeln;" and about Trigla (p. 538), "Schwimmblase wie bei Prionotus:" "Schwimmblase meist mit seitlichen Muskeln und in zwei Theile gespalten." Without knowing that this fact had already been stated by Dufossé,[1] I drew the obvious conclusion that Trigla and Dactylopterus also produce their sounds by means of the air-bladder, and that Prionotus was a sound-producing fish. In no other genera except these three muscles (extrinsic or intrinsic) were mentioned. But from what was stated about the form of the organ in the different genera, I arrived, by means of a vague conclusion, it is true, at the mere preliminary supposition with regard to twenty-six other genera or families, that the air-bladder might act as a sound-producing organ.

I am not going to fatigue the reader with a detailed account, but I shall confine myself to remarking that this idea proved correct,[2] so that, by means of my own investigations as well as by those of my predecessors, and more especially those of Dufossé, I was able to establish the following general thesis (II*b*, p. 182):—"*Where the air-bladder is a sound-producing organ, this organ is rendered the more effective, the thicker its walls are; the stronger or more elastic they are; the more it is divided into chambers* (and it is without any importance whether this division is brought about by external diverticula or by internal septa); *the more vigorous the musculature is*, and, in consequence, *the more closely it is connected with the skeleton*, provided the musculature be not intrinsic muscles. When these conditions are found together, we may determine an air-bladder as an organ producing sounds. As yet, however, with the restriction, *that the air-bladder must be either closed or furnished with a long, narrow, thin-walled pneumatic duct.*

For when the pneumatic duct is short and wide, and opens into the œsophagus with a fissure-like aperture, the *possibility* is

[1] The paper of Dufossé, dealing with this matter, was published in 1874, when I was a soldier, and I left Denmark in 1876, having never before been engaged in independent anatomical examinations of fishes.

[2] Among the twenty-six genera (or families) species producing sounds were known, or are now known: the Sciænoidei, Batrachus, Polypterus, Ceratodus, Lepidosiren, and Protopterus; muscles (extrinsic or intrinsic) were known in Therapon, Holacanthus, the Sciænoidei, Batrachus, Amblyopsis, Heterotis, Gymnarchus, Amia, Polypterus, and Lepidosiren.

not excluded, that this pneumatic duct may be capable of admitting the passage of the atmospheric air to and from the air-bladder, and in this case, therefore, it is possible that the latter may operate as an organ of respiration.

Besides the fishes, of which the anatomy is known to me through autopsy (Polypterus and Acipenser), information may be found in literature that the pneumatic duct is short and wide in Protopterus, Ceratodus, Spatularia, Arapaima (Sudis); Gymnarchus, Heterotis, Lepidosteus, Lepidosiren (in which four genera, according to the examinations of Hyrtl, the air-bladder is provided with muscles), as well as in Amia (in which, according to Franque, the air-bladder is provided with muscles). Now, it is true that several authors, on account of the anatomical data, have declared the air-bladder to be a lung in the following genera:—Arapaima (Sudis), Polypterus, Lepidosteus, Amia, Ceratodus, Protopterus, and Lepidosiren. But though it has, indeed, been observed that these fishes—with the exception of Polypterus[1]—are inhaling atmospheric air, still it is worth remarking that there exists no proof whatever[2] of the atmospheric air, respired by these fishes, being carried down into the air-bladder, as is absolutely necessary if the air-bladder is to be considered an organ of respiration.

In my book (II*b*, pp. 183–204) I have proved, as far as I can judge, that the reasons for attributing to the air-bladder the function of a lung, are anything but satisfactory. As I am here addressing myself to English-speaking naturalists, I shall confine myself to mention the Ceratodus and Protopterus, as these fishes have been repeatedly treated in English literature. The idea of attributing to the air-bladder the function of a lung arises from the *Lepidosiren paradoxa*, whose gills are so few and so small that most probably they cannot be sufficient to provide for the respiration of the animal. When this remarkable fish

[1] A sister of mine, Mrs Ida Leschly, who spent some years in Egypt, obtained information about the biology of this fish from the Egyptian fishermen. They unanimously stated this fish to live at the bottom of the river, and none of them ever saw an "Bichir" rising to the surface of the water to respire (whereas they were fully aware of the fact that such was the habit of the genus Clarias). One fisherman declared that he had heard it producing sounds in the water, but never out of it. Out of the water it is said to live only a few hours, though it is very tenacious of life.

[2] I must here remark that I have not followed these questions since 1884.

was treated in literature, no air-breathing fishes were known except the Cobitis; hence it was quite natural that, in the discussion on the Lepidosiren, no attention was paid to this isolated fact, the more so as this discussion turned chiefly upon its systematic position,—for, as is well known, it was considered by many naturalists as belonging to the Batrachia. No wonder, therefore, that the authors immediately agreed on the suggestion, that on the "lung," as it was called, was ingrafted the function of a respiratory organ. However, the probability that the air-bladder is really acting as a lung in this animal is somewhat confirmed by Dr Bohls[1]—

"Die Bedeutung der Lunge als Respirationsorgan kennzeichnet sich bei den lebendfrisch geöffneten Tieren durch die hellrote Farbe, die sie dem arteriell gewordenen Blut verdankt." When the author adds: "Die von mir gehaltenen *knurrten* beim Anfassen, ein Laut, der erzeugt wurde durch Auspressen der Luft aus den engen Kiemenöffnungen."

This explanation of the manner in which the sounds are produced appears to me rather doubtful.

The question was then proposed if the air-bladder was not to be considered a respiratory organ in other fishes, where it is cellular. Joh. Müller, meeting with an air-bladder of this kind in some Siluroidæ and in Erythrinus, thought fit[2] to reduce the question to a more definite form, and he answered it to the effect that the air-bladder in the Lepidosiren was to be considered a respiratory organ because of its receiving ("dark") blood from and returning ("light") blood to the heart, but that this was not the case either in the Polypterus, the organ in this fish receiving blood from the fourth gill-vein, and returning blood to the liver-veins, or in the Erythrinus, where it received blood from the arteries of the body, and returned blood to the veins of the body. This distinction, which is obviously founded on relations in the superior Vertebrata, was generally adopted, and is still considered decisive—thus Moreau calls it "les justes remarques." And yet it is incorrect, nevertheless. For the

[1] Bohls, "Mittheilungen über Fang und Lebensweise von Lepidosiren aus Paraguay," *Aus. d. Nachricht d. k. Ges. d. Wiss.*, Göttingen, 1894, No. 2.

[2] VIIIc: Müller, Joh., "Untersuchungen über die Eingeweide der Fische: Schluss der vergleichenden Anatomie der Myxinoiden" (*Abh. d. k. Akad. d. Wiss. zur Berlin*, A. d. J. 1843, Berlin, 1845, pp. 109–170).

physical principle of respiration is, that the blood enters into so close a relation with the air (atmospheric air, or air absorbed in water) that by a diosmosis a change of matter may be effected between the air in the blood and that without. And it is of no consequence whether the respiring capillaries are ramifications of an artery or of a vein. Consequently, an animal is able to respire with any part of its body provided that this part can enter into contact with the air: the outer skin, the cavity of the mouth, the gill-cavity, the intestines, the gills, or the lung. That the skin in Fishes shares in the respiration has already been shown by Spallanzani,[1] Provençal and Humboldt.[2] To what degree it shares in this function has not yet been proved, as far as I know; probably it does so in a rather great measure. But, on the other hand, respiration cannot take place when the air which, having been in contact with the respiring part of the body, has been rendered incapable of continuing the respiration, is not replaced by fresh air—that is, provided the respiring superficies is placed inside the body (gills, lung, intestines), by mechanical respiration. Whether an internal organ is an organ of respiration may therefore be decided by examining if it is the seat of mechanical respiration, which is, to a certain extent, constant, and whose continuation is necessary for the animal's existence, at least under certain circumstances. If we confine ourselves to the air-bladder, it has already been proved by Delaroche at the beginning of this century, and still more conclusively by Moreau, that there exists a constant exchange between the air in the air-bladder and the air in the blood,[3]

[1] Spallanzani, L., *Mémoires sur la respiration*, traduits par J. Senabier, Genève, 1803, pp. 113–114.

[2] IX. Provençal et Humboldt, "Recherches sur la réspiration des poissons," p. 392 (*Mémoires de physique et de chimie, de la société d'Arcueil*, T. II., Paris, 1809, pp. 359–404).

[3] The quantity of carbonic acid is variable. According to Moreau, in Perca, when normal, scarcely 1 per cent. is found, and in Barbus $\frac{1}{2}$ per cent.; but the author, who unfortunately gives no details of his examinations, says in general: "Les proportions d'acide carbonique sont généralement au-dessous de 10 per cent. et même au-dessous de 5 pour 100." Schultze, Fr. ("Ueber den Gasgehalt der Schwimmblase einiger Süsswasserfische Deutschlands." *Pflüger's Archiv. f. d. gesammte Physiologie*, V. Bonn, 1872, p. 48–52), found in Barbus 1·4–4 per cent., and in Tinca 3·9–5·4 per cent. Schultze pretends to be, in 1872, the first author who has found the carbonic acid in the air-bladder. Without being thoroughly versed in this question, I know several authors previous to Schultze

and yet it is no organ of respiration. It cannot be called so unless its air is renewed by mechanical respiration. If that be the case, it is an organ of respiration, no matter whence its blood comes and where it goes. Not to mention that (according to Hyrtl) the accessory gill-cavity in Saccobranchus receives some vessels from (and returns to) the adjoining parts of the body, and that (according to Jobert) the intestinal tube in Callichthys receives blood from the aorta, the venæ cavæ, and the vena porta renalis, there is another fact, pretty well known, which has no reference to the Fishes, which proves the untenability of the distinction set up by Joh. Müller. It is a well-known fact that the inwardly smooth hinder part of the lung in Snakes and in certain Sauria receives blood from the aorta. In accordance with the distinction of Joh. Müller, this fact is constantly interpreted to the effect that the hind part of the

who have made this observation. Moreau found carbonic acid in several Fishes ("Sur l'air de la vessie natatoire des poissons." In *Compt. rend. d. l'Acad. d. Sci.*, T. LVII., Paris, 1863, pp. 816–20). Humboldt found 2 per cent. in Exocœtus (*Reise in die Aequinoctial-Gegenden des neuen Continents*, I. Stuttgart, 1859, p. 179) and 4 per cent. in Poecilia Bogotensis (Humboldt et Aimé Bonpland: *Recueil d'observations de zoologie et d'anatomie comparée . . .*" T. II., Paris, 1833, p. 155). Provençal et Humboldt, in 1809, found 5·2 per cent. in Cyprinus carpio (IX., p. 401), and in 1789 Fourcroy found carbonic acid in Cyprinus carpio ("Observations sur le gaz azote contenu dans la vessie natatoire de la carpe" . . . in *Annales de Chimie*, I., Paris, 1789, pp. 47–51). If the author had consulted Cuvier, *Leçons d'anat. comp.*, he would have found (Edit. 2, T. VIII., p. 724) two of the authors mentioned, to whom I have referred here. When he says with regard to the two authors Biot and Erman, with whose papers he has made himself acquainted: "Dass die älteren Beobachter fälschlich einen vollständigen Mangel von CO_2 behauptete, eine Thatsache, die ihnen allerdings unerklärlich schien, die sie aber als solche hinnahmen," then he must have perused their papers rather superficially. For Biot ("Mémoire sur la nature de l'air contenu dans la vessie natatoire des Poissons," in *Mém. de phys. et de chim. d. l. soc. d'Arcueil*, T. I., Paris, 1807, pp. 254–281) says, p. 259: "Je n'avois pas . . . les moyens nécessaires pour mesurer exactement la quantité d'acide carbonique, . . . mais je me suis du moins assuré que cette quantité est fort petite." Dr. Schultze doubts the correctness of Biot's observations that the air-bladder in Fishes captured in the sea at a deep level contains great quantities of oxygen. Delaroche and Moreau, too, have proved the correctness of these observations to be beyond all doubt. Moreau (VI., pp. 79–84) has also shown that it is under the influence of the N. vagus that oxygen is received into the air-bladder. Dr. Bohr, Professor of Physiology at our university, has made experiments on the same subject, and has shown "that the formation of gas in the air-bladder is a true secretion of a highly oxygenated gaseous mixture, and that the secretion is so far under the control of the nervous system that it fails when the branches of the vagus which supply the air-bladder are cut" (*Jour. of Physiology*, vol. xv., No. 6, 1893, pp. 494–500).

lung in these animals is not respiratory. But what, in this case, we do not know, is the operation carried on in the capillaries in the recording section of the lung, whereas that which we do know is, that the lung in Snakes is an organ of respiration, *i.e.*, it is by turns receiving and expulsing the air. And we have not the slightest reason for doubting that the atmospheric air reaches the hinder part of the lung, if by no other means, at any rate by diffusion, by which means the air reaches into the bronchioli respiratorii and the alveoli pneumonales in the Mammalia. If we suppose that the hinder part of the lung in Snakes is not respiratory, we have simply turned things upside down; the conclusion being drawn from what was unknown to and against what is known: and yet it has given no offence. The very same method has been adopted with respect to the pseudobranchia and opercular gills in Fishes. We continually meet with the statement that when these organs receive venous blood their function is respiratory, but when they receive blood which has passed through the gill their function is not respiratory. And this theory is still maintained though there is not the slightest reason to suppose that, even in the latter case, the function of these organs should be another than that of the gills themselves with regard to the diosmotical relations. It is of some interest to see that none of the authors, who have supposed the air-bladder in some Fish to be a lung, has cared to get a notion of the mechanism necessary for the renewal of the air.

On account of the structure of the air-bladder and the relations of its arteries and veins, Sir Richard Owen judged the air-bladder in Protopterus to be an organ of respiration. Peters,[1] who has given the fullest account of the anatomy of this fish, gives a copious description of the ramification of the blood-vessels to the gills and the air-bladder, and says as follows (p. 17):—

"Im Ursprung unterscheidet sich die Lungenarterie, wie man sieht, nicht wesentlich von andern Körperarterien, die aus der Aorta Blut erhalten, und dies könnte es zweifelhaft machen, ob die Lungen des Lepidosiren [Protopterus] wirklich Lungen sind; diese Natur

[1] Peters: Ueber einen dem Lepidosiren annectens ähnlichen Fisch von Quellimane (*Archiv f. Anat. u. Physiol.*, Berlin, 1845, p. 1).

wird aber bewiesen theils durch die directe Einmündung der Lungenvene ins Herz, theils und noch bestimmter [dadurch] dass aus den Aesten des Truncus arteriosus schon Körperarterien entspringen, nähmlich die oben angezeigten." But afterwards, when he had an opportunity of dissecting the living Fish, he already began to doubt, and leaned to the opposite opinion, saying :[1]—" Dass die lungenähnliche Schwimmblase, ungeachtet des besonderen Eintritts ihrer Vene in das Atrium des Herzens, dennoch kaum als Lunge fungirt, scheint mir daraus hervorzugehen, dass ich an dem lebenden Thiere keinen Unterschied in der Färbung zwischen ihrem Blute und der der Körpervene bemerken konnte."

As to the habits of this animal, we know [2] that it becomes torpid during the dry season, like a fairly considerable number of tropical fishes, as in northern countries some fishes pass the cold season immersed in the mud, in a state of torpor; that it takes in atmospheric air (" occasionally, but at uncertain periods," according to Gray—" Anfangs . . . alle 4 bis 5 Minuten," according to MacDonnell). Where the air it has taken in is respirated, is unknown; the animal appears to swallow it and to expel it again through the mouth; and that it produces sounds : " Merkwürdig war mir," says MacDonnell, " dass es von dem Moment an, da ich es in das Wasser gesetzt hatte, aufhörte Töne von sich zu geben, selbst wenn man es aus dem Wasser herausnahm."

When Dr. Günther made known to the scientific world the Australian Ceratodus, which is so curious in many respects, nothing was known of its habits but what was stated in the passage quoted below. According to his observations, the air-bladder—or, as it is called by Dr Günther, the " lung "—gives off blood to the heart, and one of its arteries can be injected from the arteria cœliaca, while no direct arterial connection exists between the air-bladder and the arcus aortæ, as in Lepidosiren. As to the manner in which Ceratodus is respiring, Dr. Günther proposed [3] the following hypothesis, exclusively based on the anatomical relations :—

[1] Peters : Reise nach Mozambique, IV. Berlin, 1868. *Flussfische*, p. 5.

[2] Peters, *l.c.*—Gray, J. E.: Observations on a living African Lepidosiren in the Crystal Palace (*Proc. of the Zool. Soc.*, London, 1856, p. 343–48).—MacDonnell, R.: Notiz über Lepidosiren annectens (*Zeitschr. f. wiss Zool.*, X., 1860, p. 409–11).—Duméril, A.: Observations sur des Lépidosiréniens (*Compt. rend. d. l'Acad. d. Sci.*, T. LXII. Paris, 1866, p. 97).

[3] Günther, Albert : Description of Ceratodus, . . . (*Phil. Trans. Roy. Soc.*, London, 1871, Pt. II., p. 511–571, p. 542).

"I think it much more probable that this animal rises now and then to the surface of the water in order to fill its lung with air, and then descends again until the air is so much deoxygenised as to render a renewal of it necessary. The Fish is said to make a grunting noise, which may be heard at night for some distance. This noise may be produced by the passage of the air through the œsophagus,[1] when it is expelled for the purpose of renewal. *From the perfect development of the gills we can hardly doubt that, when the fish is in water of normal composition, and sufficiently pure to yield the necessary supply of oxygen, these organs are sufficient for the purpose of breathing, that the respiratory function rests with them alone,* and that the lung receives arterial blood, returning venous blood, like all the other organs of the body. *But when the Fish is compelled to sojourn in thick, muddy water, charged with gases, which are the product of decomposing organic matter*[2] (and this must be the case very frequently during the droughts which annually exhaust the creeks of tropical Australia), *it commences to breathe air with its lung in the way indicated above.* Under this condition the pulmonary vein carries purely arterial blood to the heart, where it is mixed with venous blood and distributed to the various organs of the body. *If the medium in which the Fish happens to be is perfectly unfit for breathing, the gills cease to have any function;* if only in a less degree, the gills may still continue to assist in respiration. Ceratodus, in fact [in fact ? !], can breathe by either gills or *lungs alone*,[3] or by both simultaneously."

What is the foundation of the suggestion propounded by Dr. Günther? It is true, he does not tell us so himself, but it is obvious that it is founded on two facts—that the air-bladder is cellular,[4] and that it sends its blood to the atrium of the heart;

[1] In these words the suggestion propounded by Joh. Müller (VII.) is seen to reappear.

[2] But if so, the Fish would, I think, nevertheless be lost, even if it were able to continue the respiration. While I stayed at Rio Paraguay a most extraordinary inundation took place; at that time it was quite a common view to see dead or dying Fishes near the riverside—in the midst of the stream I never saw any. That they had been poisoned by products of decomposition of putrefying organic matter, I could not doubt. Such matters are likely to be absorbed through the skin, a circumstance that Dr. Günther seems to have quite overlooked. That the lateral line serves to inform the Fish of the nature of the water, is no mere conjecture; that it is at least partly an organ of taste, is most certainly proved.

[3] This statement does not, however, agree too well with another passage of the author (p. 541): "the terminal branches of both arteries and veins [of the air-bladder] are rather wide, and can be injected with great facility."

[4] The remarkably well-drawn figure of the air-bladder in Dr. Günther's work (Pl. XXXVIII. fig. 2) shows me a structure which bears the greatest resemblance to air-bladders, that are sound-producing organs. But for the above-mentioned reason, I dare not—even as supposition—advance the opinion that this is the organ by which the animal produces the sounds which it is known to emit.

perhaps his suggestion that the air-bladder acts as an organ of respiration is right, perhaps it is wrong. I observe that Dr. Günther does not refer to the highly interesting and excellent investigations of Day (X*a*),[1] published three years before, on air-breathing fishes of India.

As to the biology of Ceratodus, we have, as far as I know, only a short report in a letter from E. Pierson Ramsay,[2] who kept some living specimens in the Australian museum at Sydney. And his report does not prove its breathing atmospheric air; for though he kept them "in a large tank," he does not say a word of their taking in air, but "when it rests on the bottom of the tank the pectorals are placed at nearly right angles to the body, the posterior fins lying parallel to the tail. If not disturbed they will remain in this position for hours, and only when stirred up think it necessary to use their fins and tail at all." For though it was "winter time and very cold," this behaviour offers a complete contrast to the proceeding of real air-breathing fishes, with regard to which Day says (X*a*, p. 275):—". . . . . the purely water-breathers, if the term is admissible, can live without rising to the surface, unless under peculiar circumstances, whilst the compound breathers, as already mentioned, expire in a longer or shorter period if unable to reach the atmospheric air," whilst in another place (X*b*., p. 205)[3] he says:—"Of course under certain *abnormal* conditions, all species [of Fishes] rise to the surface, as I have already pointed out." I have lately seen in *Zoologischer Anzeiger* a notice on a work of R. Semon, "Zoologische Forschungsreise in Australien und dem Malayischen Archipel," the first volume of which work deals with Ceratodus. After the few words, added as a summary, the notice goes on to say:—"Das Tier atmet einmal in 30–40 Minuten." The work itself I have not seen as yet; it is to be hoped that the author, who has had an opportunity of studying the animal in its native habitat, has been able to give conclusive information whether the air taken in by the animal is respired in the air-

[1] X*a*: Day, Fr., "Observations on some of the Freshwater Fishes of India" (*Proc. of the Zool. Soc.*, London, 1868, pp. 274–288).

[2] *Proc. of the Zool. Soc.*, London, 1876, pp. 698–99.

[3] X*b*: Day, Fr., "On Amphibious and Migratory Fishes of Asia" (*Journ. of the Linn. Soc.*, London, vol. VIII., 1878, pp. 198–215).

bladder, or, as is the case in so many other Fishes, in the intestines, or in some other organ.

Posterior to Dr. Günther, a German author, Dr. Boas,[1] has found that the air-bladder in Ceratodus receives blood from the 4th gill-vein. Why the author considers the air-bladder to be a "lung" he does not tell us. But to him the circulation of blood in the organ cannot have been conclusive, as he regards the air-bladder as a lung, not only in Ceratodus and Protopterus, but also in Amia,[2] Lepidosteus,[3] and Polypterus,[4] although these fishes afford a striking contrast in that respect: for in some (in Ceratodus, according to Boas, and in Polypterus) the organ receives its blood from one pair, in others (Amia) from two pair of gill-veins; in others (Lepidosteus) from the aorta; and it returns it, now to the atrium of the heart (Ceratodus and Protopterus), now again to the kidneys (Lepidosteus), or the liver (Polypterus), or to the veins of the body (Amia, according to Franque). Accordingly, as it cannot be the relations of the blood-vessels that have determined the suggestion of this author, it must have been the circumstance that in all these forms the air-bladder is very cellular; thus his view is essentially older even than Joh. Müller.

Now, I am well aware that most readers will shake their heads at my presuming to question the accuracy of the generally adopted opinion that the "Dipnoi" respire by means of their air-bladder. But in order to point out how difficult it is to get a thorough knowledge of the function of an organ by mere

[1] Boas, J. E. V., Ueber Herz und Arterienbogen bei Ceratodus und Protopterus, *Morphol. Jahrbuch*, VI., 1880, p. 321–354.

[2] This animal is well known to take in atmospheric air (Wilder, B. G., in *Proc. Amer. Asso. Adv. Sci.*, 1875, Salem, 1876, p. 151 ; *ibid.*, 1877, p. 306–313); "Aereal Respiration in the Mud-Fish," in *Proc. Bost. Soc. Nat. Hist.*, XIX., 1878, p. 337 ; but we ignore by which organ it respires the air.

[3] Poey, F. (Memorias sobre la historia natural de isla de Cuba, T. II., 1856–58, p. 69), and B. G. Wilder (in his first quoted paper), have found that also this Fish takes in atmospheric air ; but it is unknown in which organ it is respired. The observation of Poey is incorrectly referred by A. Duméril (*Hist. Nat. de Poissons*, T. II., 1870, p. 300).

[4] In a later paper (Ueber den conus arteriosus und die Arterienbogen der Amphibien. In *Morphol. Jahrbuch*, VII., 1882, pp. 488–572) Dr Boas has not included Polypterus among the Fishes which he supposes to breathe by means of a "lung." The reason (which the author has forgotten to tell his readers) is, that I myself informed him personally of the above-mentioned features of the habits of this Fish.

anatomical examinations, even if only mechanical principles are in question, I shall recall to the memory of my readers how the theory of Borelli as to the air-bladder as a hydrostatic apparatus was considered a fact beyond all contradiction, and yet it was crushed when put to the first[1] serious experimental test. Nay, even a thing so plain in appearance as the effect produced on an organ by the contraction of a muscle may be misinterpreted: not only Bridge and Haddon, but even a prominent author like Joh. Müller has been of opinion that the powerful extrinsic muscles of the air-bladder in the Pimelodina would by their contraction effect a compression of the organ, while the fact is that they effect an expansion, be it even momentary, of the said organ. And I do not doubt but that a reader who is not versed in the literature in question would, in perusing the physiological section of the work of Professors Bridge and Haddon, be filled with admiration at the acuteness and close reasoning displayed—and yet scarcely one passage is correct, because they have not examined the said organs in living specimens, and because they had but an insufficient knowledge of the literature in which are deposited the results of that kind of investigation.

It is worth remembering that in the air-breathing fishes, in which the matter is *well* known, it is not in the air-bladder that the respiration of the inhaled air takes place. Not to mention some of our European Cyprinoidæ, *e.g.*, *Carassius vulgaris*, which in the summer time, when the water is getting deficient in oxygen (if they live in smaller ponds), try to remedy this want by letting the atmospheric air pass, together with the water, over their gills, it is well known in the European species of the Cobitini that the respiration of atmospheric air, which frequently takes place when these fishes are chased out of the mud, where they use to live almost without stirring, though now and again, with long intervals however, they resort to the surface to take in atmospheric air, is brought about by the intestine.[2] The

[1] Valenciennes (XV., vol. xvi., 1842, pp. 14–16) had made experiments to empty the air-bladder of air in *Gobio fluviatilis* and he had seen it "très doucement" filled with air in the course of some hours, without the animal taking in atmospheric air. But Valenciennes did not see the bearing of his own observation.

[2] Erman, in his excellent paper, Untersuchungen über das Gas in der Schwimm-

same fact has been established, according to Jobert,[1] in Hypostomus sp. (XI*b*), Callichthys asper (XI*a*), Doras sp. (XI*b*), and Loricaria sp. (XI*a*), which Fishes cross the land to reach other waters, when their former dwelling-places are growing short of water. In his interesting investigations on several air-breathing Fishes of India, Day (X*a* and X*b*) has proved that the respiration of the atmospheric air is brought about in the labyrinthiform part of the gill-cavity in Polyacanthus, Osphromenus, Trichogaster, Ophiocephalus, and Rhyncobdella. The same author has pointed out that the air is respired in the accessory gill-cavity of Clarias,[2] Saccobranchus, and Amphipnous. The existence of an accessory "gill-snail" (Kiemensschnecke) has been proved by Hyrtl[3] in Heterotis Ehrenbergii, Chanos ("Lutodeira chanos"), Meletta thryssa, Chatoessus jacunda, Gonostoma Javanicum, Clupanodon aureus, Pellona Lechenaultii, and Hyodon claudalus, and an organ of a similar structure has been found by Kner[4] in Cœnotropus labyrinthicus, Curimatus vittatus, and C. cyprinoides. Most probably this organ is an air-breathing organ; however, before the year 1884, no physiological proof existed of this being the case.

When I said above that an air-bladder without a pneumatic duct, or with a long, narrow, and thin-walled pneumatic duct, may be determined as a sound-producing organ (according to our present knowledge), when furnished with extrinsic or intrinsic muscles, especially when its cavity is divided into inter-com-

blase der Fische, und über die Mitwirkung des Darmkanals zum Respirationsgeschäfte bei der Fischart Cobitis fossilis (*Gilbert Annalen der Physik.*, XXX., Halle, 1808, pp. 113–161).

[1] XI*a*: Jobert, Recherches pour servir à l'histoire de la respiration chez les Poissons (*Ann. d. Sci. Nat.*, 6 Sér., T. V., Paris, 1877, Art. No. 8).—XI*b*: Jobert, Recherches anatomiques et physiologiques pour servir à l'histoire de la respiration chez les Poissons (*ibid.*, 6 Sér., T. VII., Paris, 1878, Art. No. 5).

[2] I myself, who did not then know of the examinations of Day, have made the same at least almost evident with regard to Clarias macracanthus from the Nile (Om Aandedrœttet hos Clarias [On the Respiration in Cl.]. In *Naturhistorisk Tidskrift*, 3 R., Bd. XIII., Kjöbenhavn, 1883, p. 396–414).—What I there have said on the nature of the gill-rakers of Clarias is wrong.

[3] Hyrtl, J., Beitrag zur Anatomie von Heterotis Ehrenbergii (*Denkschr. d. k. Akad. d. Wiss. in Wien*, Bd. VIII., 1854, p. 74).—Hyrtl, J., Ueber besondere Eigenthümlichkeiten der Kiemen und des Skelette, und über das epigonale Kiemenorgan von Lutodeira (*ibid.*, Bd. XXI., 1862).

[4] Kner, R., Ueber Kiemen-Anhänge bei Characinen (*Ver. d. Zool-bot. Ges. in Wien*, 1861, p. 189).

municating chambers, I must point out that some naturalists have succeeded in proving, with regard to some Fishes, that the air-bladder serves to produce tones, even if it is *not* provided with special muscles. This fact has been proved by Dufossé, by means of vivisection of the animals, in *Peristedion cataphractum Trigla lyra, Hippocampus brevirostris, Sciœna aquila*, and *Umbrina cirrhosa*. In these Fishes the air-bladder sounds during the activity of the muscles, with the fascia of which the walls of the air-bladder are intimately connected. In these Fishes the conditions, at least according to the indications of Dufossé, are such that it would hardly have been possible to any one, by a mere anatomical examination, to recognise the air-bladder as a sound-producing organ. But, on the strength of Dufossé's physiological examinations, I am of opinion that the air-bladder has the same function in *Triacanthus brevirostris* and *Tr. biaculeatus*. In the following Fishes I have succeeded, by a mere anatomical examination, in recognising the air-bladder as a sound-producing organ, though it is not provided with special muscles: *Tetrodon fahaka, Balistes vetula, Monacanthus pardalis*, and *Holocentrum sogho*, in which Fishes the walls of the air-bladder are acted on in a somewhat different way by the muscles leading to the "coracoideum" (Cuv.). Finally, Professor Möbius [1] has recognised the air-bladder of *Balistes aculeatus* as a sound-producing organ, likewise employed in sounding under the action of muscles which lead to the same bone ("Postclaviculare"). And while I had arrived at the said result through anatomical examination alone with regard to the above-mentioned species of this genus, Professor Möbius had the opportunity to observe in *B. aculeatus*, in the living animal, "while the fish was drumming, a quick raising and sinking of a small spot of the skin," which spot proved by the following anatomical examination to be in immediate contact with part of the wall of the air-bladder.

[1] XII: Möbius, K., Balistes aculeatus, ein trommelnder Fisch. (*Sitzber. d. Akad. d. Wiss.*, Berlin, Bd. XLVI., 1889, p. 999–1006). Zacharias, Otto, "Trommelnde Fische" (I have but seen a copy of this short paper, four pages) contains no independent investigations, but is only a popular report of the paper of Möbius.

(*To be continued.*)